

# The effect of sea temperature on seagrasses and algae on the Western Australian coastline

D I Walker

Botany Department, The University of Western Australia, Nedlands, WA 6009, Australia

## Abstract

Macroalgae and seagrasses are the important primary producers on the West Australian coastline. As benthic organisms, they are effective integrators of the environment, but their presence at a particular location is the result of two different processes - 1) Dispersal and settlement and 2) Growth. The Leeuwin Current may affect both these processes, through its transport of reproductive material (both vegetative and sexual) and its effect on water temperatures.

Direct effects of the Leeuwin Current on the marine flora of south west Western Australia are less detectable than its effects on marine animals. Marine macroalgae show only sporadic tropical influence, with the flora being dominated by southern temperate species. The Leeuwin Current does affect tropical seagrass species in WA by extending their southern latitudinal distribution limits.

The west coast of Western Australia is very different to the east coast of Australia and to the west coasts of South Africa and South America. Macroalgae are particularly influenced by the prevailing currents and upwellings, and the Western Australian coast does not have the large, cool temperate kelps present on the other two continental west coasts. The absence of seagrasses from both these west coasts would seem to be a consequence of lack of habitat availability for seagrasses.

## Introduction

Macroalgae and seagrasses are important benthic primary producers on the Western Australian coastline. They represent very different types of organisms - algae belong to the Kingdom Protista, and there are ca 8500 marine species world-wide, whereas seagrasses are a very specialised group of about 50 species of angiosperms that have reinvaded the marine environment. However, requiring light for photosynthesis, they are both found in relatively shallow water, and play similar roles in their coastal habitats. As benthic organisms, they are effective integrators of the environment, but their presence at a particular location is the result of two different processes:

1. Dispersal and settlement
2. Growth

The Leeuwin Current, which brings warm tropical water down the west coast of Australia in winter (Pearce 1991) may affect both these processes, through its transport of reproductive material (both vegetative and sexual) and its effect on water temperatures.

Macroalgae occur on rocky substrata, with a variety of water movement conditions. Their depth range is from the intertidal to about 50 m, although this may be greater in clear offshore areas, and less in more turbid

inshore waters. Some 360 species have been recorded from Rottnest Island (Huisman & Walker 1990), but the total for the Western Australian coast is probably about 700.

The main habitats for seagrasses are very extensive shallow sedimentary environments that are sheltered from oceanic swell, such as embayments (eg Shark Bay, Cockburn Sound), protected bays (eg Geographe Bay, Frenchman's Bay) and lagoons enclosed by fringing reefs (eg Bunbury to Kalbarri). Seagrasses occupy approximately 20 000 km<sup>2</sup> on the Western Australian coast (Kirkman & Walker 1989), ranging in depth from the intertidal to 45 m (Cambridge 1980), making up a major component of nearshore ecosystems. The diversity of seagrass genera (10) and species (25) along this coastline (Table 1) is unequalled elsewhere in the world (Walker & Prince 1987).

## Temperature and Biogeography: Macroalgae

In general, the rocky sub-tidal environment of south-west Western Australia has extensive populations of the kelp *Ecklonia radiata* and *Sargassum* spp. Mixed macroalgal assemblages of foliose red, green and brown algae also occur, particularly on convoluted limestone reef substrata. As the substratum changes from limestone to granite at Cape Naturaliste, cold temperate brown algae become much more

conspicuous. However, the Western Australian coast does not possess large kelps such as *Macrocystis*. To the north, the kelp disappears and more tropical genera and species become dominant eg *Dictyopteris*. The Rhodophyta become more abundant, particularly those that calcify.

Table 1

Seagrass species found in Western Australia

<i>Amphibolis antarctica</i> (Labill.) Sonder et Aschers. ex Aschers.
<i>Amphibolis griffithii</i> (J.Black) den Hartog
<i>Cymodocea angustata</i> Ostenfeld
<i>Cymodocea serrulata</i> (R.Br.) Aschers. and Magnus
<i>Enhalus acoroides</i> (L.f.Royle)
<i>Halodule pinifolia</i> (Miki) den Hartog
<i>Halodule uninervis</i> (Forsk.) Aschers.
<i>Halophila decipiens</i> Ostenfeld
<i>Halophila ovalis</i> (R.Br.) Hook.f.
<i>Halophila ovata</i> Gaud.
<i>Halophila spinulosa</i> (R.Br.) Aschers.
<i>Heterozostera tasmanica</i> (Aschers.) Dandy
<i>Posidonia angustifolia</i> Cambridge & Kuo
<i>Posidonia australis</i> Hook.f.
<i>Posidonia coriacea</i> Cambridge & Kuo
<i>Posidonia denhartogii</i> . Kuo & Cambridge
<i>Posidonia kirkmani</i> Kuo & Cambridge
<i>Posidonia ostensfeldii</i> Ostenfeld
<i>Posidonia robertsoniae</i> Kuo & Cambridge
<i>Posidonia sinuosa</i> Cambridge & Kuo
<i>Syringodium isoetifolium</i> (Aschers.) Dandy
<i>Thalassia hemprichii</i> (Ehrenb.) Aschers
<i>Thalassodendron ciliatum</i> (Forssk.) den Hartog
<i>Thalassodendron pachyrhizum</i> den Hartog
<i>Zostera mucronata</i> den Hartog

The southern Australian flora is well documented (Womersley 1984, 1987) and has one of the richest algal floras in the world (400 genera and 1100 species, Womersley 1984). However, the western coast has a reduced diversity in comparison to the south coast, despite the transition from the cold temperate flora to the subtropical and typically Indo-Pacific tropical flora of the northern waters. The relative absence of intensive collections and taxonomic studies of algae in the north of Western Australia does make biogeographical analyses of algal distributions difficult, but recent works by Kendrick *et al.* (1988, 1990) for Shark Bay, and Borowitzka & Huisman (ms) for the Dampier Archipelago have increased the information available for comparison. Huisman's collections from the Abrolhos Islands have also improved distribution records.

The most recent synthesis of south-western Australian algal distributions has been carried out by Huisman & Walker (1990) for Rottnest Island. They described Rottnest Island as possessing limestone reef habitats typical of the mainland coast, from Cape

Naturaliste to Kalbarri, and regarded the marine flora as representative of the mainland coastline. They carried out a biogeographic analysis of the macroalgal species present (Table 2) that showed the dominance of southern Australian species, with a relatively low representation of the tropical element. This is also true for the mainland coast.

Table 2

Biogeographic affinities of algal species recorded from Rottnest Island

Distribution	Number of species			
	Rhodo-phyta	Phaeo-phyta	Chloro-phyta	Total
Cosmo-politan	8	5	3	16
Indo-West Pacific	7	4	1	12
Tropical-Warm Temperate	18	10	12	40
Temperate	9	10	3	22
Southern Temperate	18	5	5	28
Southern Australian	114	31	25	170
West Australian endemic	40	5	3	48
Rottnest Island endemic	8	1	2	11
Total	222	71	54	347

While the Leeuwin Current may introduce the occasional tropical taxon to the flora, the floristic affinities of Rottnest Island lie clearly with the temperate southern coastline. Most "tropical" macroalgal species reported from Rottnest Island are of sporadic occurrence, suggesting that their appearance in the marine flora may be related to the variable strength of the Leeuwin Current. An interesting example is provided by Harvey (1855, p. 564), who recorded *Penicillus nodulosus* (as *P. arbuscula*) as "abundant, on shallow, sand-covered reefs at Rottnest". Presently, this species is found abundantly only much further north eg at the Abrolhos (B. Hatcher, pers. comm. 1989) or Cliff Head (Edgar, pers. comm. 1991), and has not been observed at all on Rottnest recently. Harvey's observation was made during the austral winter, when the Leeuwin Current flows most strongly, but *Penicillus* is no longer a



constituent of the marine flora of Rottnest Island at any time of year.

#### Temperature and Biogeography: Seagrasses

Seagrass distributions in Western Australia may be divided into two main types:

- 1 The southern monospecific meadows of genera with large plants of high biomass, such as *Posidonia* and *Amphibolis*, with small patches of high diversity.
- 2 The northern mixed seagrass assemblages, extensive on intertidal flats or within reef lagoons or on limestone pavements with sediment veneers.

Distributional limits of tropical and temperate seagrass species occur at different locations along the west coast, eg the tropical seagrasses *Thalassia hemprichii* and *Thalassodendron ciliatum* do not occur further south than 22°S, which is also the northern limit for *Amphibolis antarctica*; Shark Bay (26°S) is the southern limit for the tropical species *Cymodocea angustata* (McMillan *et al.* 1983), and *Posidonia australis* has its northern limit here (Walker *et al.* 1988); *Halodule uninervis* and *Halophila spinulosa* have their southern limits at Dongara (29°S) while *Syringodium isoetifolium* extends southwards to Garden Island (32°S). *Posidonia* species do not seem to have temperature related distributional boundaries as most species overlap on the south-west corner of Western Australia, where their distributions seem to be related to habitat availability.

Algal and zoological biogeographers have divided the western coastline into two main provinces, the tropical Dampierian and the temperate Flindersian (Womersley 1982). The boundary line is diffuse for marine algae and seagrasses. More recent analyses of faunal biogeography recognise a Northern Australian Tropical and a Southern Australian Warm Temperate Province with broad zones of overlap on both western and eastern coasts (Morgan & Wells 1991). The Southern Australian Warm Temperate Province, which commences at the Abrolhos Islands, extending southwards and eastwards into the Great Australian Bight, is rich in both overall diversity and species (20 species in 9 genera) and in local diversity, with up to 10 species recorded within 100 m<sup>2</sup> (Kirkman 1985). Despite the wide latitudinal range of the coast, the annual sea temperature range is remarkably small. This is due partly to the Leeuwin Current, which transports warm tropical water southwards in winter, and partly to the absence of any upwelling on the west coast of the continent. This warming may have an effect on seagrass distributions - for example, *Syringodium isoetifolium* extends to Garden Island (32°0'S) on the west coast of Australia but only to Moreton Bay (27°30'S) on the eastern coast.

Setchell (1935) suggested that temperature is the major factor controlling biogeographic distributions in seagrasses, but this hypothesis has been difficult to test around the Australian continent, in the absence of year round temperature data. Although some 'spot' temperatures are available, the information has not

been sufficiently comprehensive. Data from loggers positioned on the north-west shelf showed temperature differences of up to 4°C over a tidal cycle, and of at least 2°C between surface and bottom (20 m) (Holloway & Nye 1985, Simpson & Masini 1986). The range of water temperatures is greater in shallow coastal waters than further out to sea, with summer temperatures warmer and winter temperatures cooler near the shore. GOSSTCOMP weekly integrated sea surface temperature profiles (NOAA) have been used to indicate relative temperatures prevailing at different sites, and have been shown at Ningaloo to provide a good correlation with *in situ* mean temperatures ( $r=.996$ ) (Simpson & Masini 1986).

Comparisons of east and west coast southern limits have been made using these data and those of Rochford (1975, 1984) and Pearce (1986), and are summarised in Table 3. The tropical species *Thalassia hemprichii*, *Thalassodendron ciliatum* and *Halodule uninervis* have different latitudes for their southern limits on the west and east coasts, but have the same winter minimum sea temperature. There is a large difference in the sea temperature at the southern limits for *Halophila decipiens* and *Halophila ovalis* on the east and west coasts but the potential distribution of these plants is limited by the southern extent of land - 35°S on the west coast and 38°S on the east coast. *Syringodium isoetifolium*, *Halophila decipiens* and *Halodule uninervis* all occur further south on the west coast than the east coast.

These examples are all species with tropical affinities which suggests that the most likely influence of the Leeuwin Current on Western Australian seagrass distributions is by extending the southern latitudinal limit of tropical species. The remaining seagrass distributional limits are not correlated with either latitude or temperature. Differences in habitat available for seagrass colonisation on the east and west coasts may explain these distributions. The absence of protected lagoonal systems (potentially another influence of the Leeuwin Current) and of large embayments on the east coast results in most seagrasses being confined to estuaries on the east coast. These environments are more subject to extremes of physico-chemical factors.

One example of the anomalous effect of temperature on seagrass distribution occurs in Shark Bay. Its latitude (26°S) is sub-tropical, yet of the twelve species of seagrass in Shark Bay, the dominant species are of essentially southern distribution at the northern limit of their range eg *Amphibolis antarctica* and *Posidonia australis* (Walker *et al.* 1988). Shark Bay also contains species of tropical affinity such as *Syringodium isoetifolium* and *Halodule uninervis*, but these species occur much further south as well. Biogeographically, the seagrasses in Shark Bay may be regarded as a northern extension of the southern flora. In comparison to adjacent oceanic conditions, water temperatures in Shark Bay are subject to more extreme summer warming and winter cooling, apparent from NOAA imagery (Anderson 1986). The lower winter

Table 3

Biogeographic distribution, latitude of southern limit, winter minimum and summer maximum temperatures for seagrass species on the west and east coasts of Australia

Species	Distribution	Latitude of southern limit (°S)		Temperature (°C)					
		W	E	Summer maximum			Winter minimum		
				W	E	Diff.	W	E	Diff.
<i>Amphibolis antarctica</i>	Southern Australian	35	41	20	17	+3	17	13	+4
<i>Cymodocea angustata</i>	NW Australian Endemic	26	—	24	—	—	21	—	—
<i>Cymodocea serrulata</i>	Indo-West Pacific	16	28	28	25	+3	24	21	+3
<i>Enhalus acoroides</i>	Indo-West Pacific	16	10	28	30	-2	24	25	-1
<i>Halodule pinifolia</i>	Indo-West Pacific	16	19	28	27	+1	24	22	+2
<i>Halodule uninervis</i>	Indo-West Pacific	26	28	24	25	-1	21	21	0
<i>Halophila decipiens</i>	World-wide in tropics and subtropics	32	38	22	18	+4	18	14	+4
<i>Halophila ovalis</i>	Indo-West Pacific	35	38	20	18	+2	17	14	+3
<i>Halophila ovata</i>	Indo-West Pacific	26	19	24	27	-3	21	22	-1
<i>Halophila spinulosa</i>	NE, W Australia, Indonesia, Malaysia, and Philippines	28	28	24	25	-1	19	20	-1
<i>Posidonia coriacea</i>	SW, S. Australia	35	37	20	19	+1	17	15	+2
<i>Syringodium isoetifolium</i>	Indo-West Pacific	32	28	22	25	-3	18	21	-3
<i>Thalassia hemprichii</i>	Indo-West Pacific	21	19	27	27	0	22	22	0
<i>Thalassodendron ciliatum</i>	Indo-West Pacific	22	20	27	27	0	22	22	0

minimum may allow greater persistence of temperate species, particularly *Amphibolis antarctica*, which releases its viviparous seedlings in winter. These seedlings survive and grow better at lower temperatures (10-15°C) (Walker, unpubl. data 1991).

#### Contrasts between flora and fauna distributions

Marine invertebrates (Morgan & Wells 1991) and fish (Hutchins 1991) show strong tropical influences, particularly on the west and south sides of Rottnest. In contrast, the algae and seagrasses show much less strong trends. As discussed already, this may be an effect of habitat availability, but it probably also results from a difference in the dispersal mechanisms of the different types of organisms. Unlike animals with planktonic larvae, the propagules of algae are generally much-shorter lived (Suto 1950, Kain 1964) and most settle within a short distance of their source (Hoffman 1987). Van den Hoek (1987) suggested that there is no evidence that there is long distance planktonic dispersal of benthic algal spores, although it may occasionally occur, but that there is more evidence for long-range dispersal by drift algae, particularly for positively buoyant algae such as *Sargassum* and any attached epiphytes. *Sargassum* species are often widely-distributed (Womersley 1987) and, for example, *Sargassum decurrens* occurs at Rottnest Island (32°S) and around the northern Australian coast to Keppel Bay (23°S) in Queensland. This may be a consequence of the southerly flow of the Leeuwin Current. The potential for transport of algal propagules by the

Leeuwin Current is reduced in comparison to invertebrate larvae, but there is the potential for algal drift to result in range extensions as a consequence of the Leeuwin Current.

Seagrasses produce seeds or viviparous seedlings which survive longer than algal spores and so have some potential for dispersal. Successful recruitment from these seeds or seedlings, however, is rare on a local scale, as most extension of large temperate seagrass meadows is by vegetative spread (Tomlinson 1974), and there have been no reports of long-distance transport by currents. It is possible that extensions of distribution could occur in a stepped process, but the Leeuwin Current mainly flows well offshore, and may only occasionally touch the coast at different locations. Inshore currents are governed by winds. In summer the southerly influence causes northerly flowing water, while in winter both southerly and northerly flows occur.

The effects of increased winter water temperatures on algal and seagrass survival, productivity and reproductive capacity are completely unstudied. Most coastlines elsewhere in the world have a much larger temperature range, and most species of algae are regarded as being tolerant of a greater range than is found on the Western Australia coastline (van den Hoek 1982). Given the shallow habitats in which they live, and the more extreme fluctuations occurring in these habitats, the potential for the Leeuwin Current to increase the winter minimum is likely to have only a marginal influence on species at the limits of their distribution.





Fig 1a. The overall distribution of Indo-West Pacific species - *Syringodium isoetifolium*, *Thalassodendron ciliatum*, *Thalassia hemprichii* and *Enhalus acoroides*.



Fig 1c. Southern Australian species such as *Amphibolis antarctica* and *Posidonia australis*.



Fig 1b The distributions of *Zostera capensis* (▲) and *Heterozostera tasmanica* (●).



Fig 1d *Zostera marina*

Figure 1. Maps of global seagrass distribution. Each map shows the extent of the generalised distribution. For precise distributions of Western Australian species, consult Table 1, for other species, den Hartog (1970) and Phillips & Menez (1988).

### Comparisons with South Africa and South America

Both South Africa and South America have extensive subtidal kelp forests particularly on their west coasts, and also have mixed macroalgal assemblages. In South Africa, the combined effects of the Benguela Current and the most intense, clearly defined upwelling in the world result in very cold waters and occasional extreme temperature fluctuations of 10°C in 7 hours (Branch & Branch 1981). Kelp forests of *Ecklonia maxima* and *Laminaria pallida* dominate. The South American coast extends much further south and has extensive forests of *Durvillaea antarctica* and *Lessonia nigrescens* (Santelices *et al.* 1980) in Chile and *Macrocystis integrifolia* and *M. pyrifera* also occur.

Both South Africa and South America show conspicuous absences of seagrasses from their west coasts (Fig. 1). Seagrasses have been recorded from the east coast of Brazil (De Oliveira *et al.* 1983), and there is one record of a small meadow of *Heterozostera tasmanica* from Coquimbo, Chile (30° 16'S) (Phillips *et al.* 1983) and a recent range extension to Caleta Chascos (27°40'S) (Gonzalez & Edding 1990) (Fig. 1b).

Aside from this the South American west coast has no seagrass reported over a distance of some 9000 km and, although records are scarce, the habitats are generally unsuitable, again with a rocky shoreline and a relative absence of large sheltered embayments. There are some embayments at high latitudes in Chile, but unlike the extensive Alaskan populations of *Zostera marina*, (Fig. 1d) these southern hemisphere areas are not known to support seagrass meadows.

The Indo-Pacific tropical species are present on the north east coast of Africa (Fig 1a), but decline in species richness and abundance towards South Africa (Phillips & Menez 1988). No seagrass species are reported below about 10°S on the west coast, except *Zostera capensis* which occurs in estuaries around the Cape of Good Hope and up to the mouth of the Orange River (Fig 1b). The west coast of South Africa has not been glaciated and has few large estuaries, although there is extensive sediment movement associated with the Benguela Current, and the Orange River contributes huge amounts of sediment when in flood. The absence of seagrasses would seem to be due mainly to the lack of sheltered habitat.

## Conclusions

The effects of the Leeuwin Current on the marine flora of Western Australia are less detectable than its effects on marine animals. Marine macroalgae in south-western Australia have only sporadic occurrences of tropical species, with the flora being dominated by southern temperate species. The Leeuwin Current does affect tropical seagrass species in WA by extending their southern latitudinal distribution limits.

The west coast of Western Australia is very different to the east coast of Australia and to the west coasts of South Africa and South America. Macroalgae show similarities between the latter coasts, and are influenced by the prevailing currents and upwellings. The absence of large scale seagrass meadows from both the other west coasts would seem to be a consequence of lack of habitat availability for seagrasses.

*Acknowledgements:* Gary Kendrick provoked some interesting ideas about dispersal and the South American west coast. This manuscript was improved by comments from Arthur McComb and Hugh Kirkman. Ainsley Calladine assisted in the production of Figure 1.

## References

- Anderson P K 1986 Dugongs of Shark Bay, Australia - seasonal migration, water temperature and forage. *National Geographic Research* 2: 472-490.
- Branch G & Branch M 1981 *The living shores of South Africa*. C Struik Publishers Cape Town.
- Cambridge M L 1980 Ecological studies of seagrass of south-western Australia with particular reference to Cockburn Sound. Ph.D. Thesis University of Western Australia 326 pp.
- de Oliveira E C, Pirani J R & Giulietti A M 1983 The Brazilian Seagrasses. *Aquat Bot* 16: 257-267.
- den Hartog C 1970 *The seagrasses of the world*. North Holland Publishing Company, Amsterdam, London. 275pp.
- Gonzalez S A & Edding M E 1990 Extension of the range of *Heterozostera tasmanica* (Martens ex Aschers) den Hartog in Chile. *Aquat Bot* 38: 391-395.
- Harvey WH 1855 Some account of the marine botany of the colony of Western Australia. *Transactions of the Royal Irish Academy* 22(Science): 525-566.
- Hoek C van den 1982 The distribution of benthic marine algae in relation to the temperature regulation of their life histories. *Biol J Linn Soc* 18: 81-144.
- Hoek C van den 1987 The possible significance of long-range dispersal for the biogeography of seaweeds. *Helgolander Meeresunters* 41: 261-272.
- Hoffman A J 1987 The arrival of seaweed propagules at the shore: a review. *Bot mar* 30:151-165.
- Holloway P E & Nye H C 1985 Leeuwin current and wind distributions on the southern part of the Australian North West Shelf between January 1982 and July 1983. *Aust J Mar Freshw Res* 36: 123-37.
- Huisman J & Walker D I 1990 A catalogue of the marine plants of Rottnest Island, Western Australia, with notes on their distribution and biogeography. *Kingia* 1: 349-549.
- Hutchins J B 1991 Dispersal of tropical fishes in temperate seas of the southern hemisphere. In: *The Leeuwin Current: an influence on the coastal climate and marine life of Western Australia*. (eds. AF Pearce and D I Walker). *J Roy Soc WA* 74:79-84.
- Kain J M 1964 Aspects of the biology of *Laminaria hypoborea*. III Survival and growth of gametophytes. *J mar biol Assoc UK* 44: 415-433.
- Kendrick G A, Huisman J M & Walker D I 1990 Benthic macroalgae of Shark Bay, Western Australia. *Bot Mar* 33: 47-54.
- Kendrick G A, Walker D I & McComb A J 1988 Changes in distribution of macro-algal epiphytes on stems of the seagrass *Amphibolis antarctica* along a salinity gradient in Shark Bay, Western Australia. *Phycologia* 27: 201-208.
- Kirkman H 1985 Community structure in seagrasses in southern Western Australia. *Aquat Bot* 21: 363-375.
- Kirkman H & Walker D I 1989 Western Australian seagrass In: *Seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*. (Eds A W D Larkum, A J McComb, S A Shepherd) Elsevier/North Holland pp 157-181.
- McMillan C, Young P C, Cambridge M L, Masini R J & Walker D I 1983 The status of an endemic Australian seagrass, *Cymodocea angustata* Ostenfeld. *Aquat Bot* 17: 231-241.
- Morgan G J & Wells F E 1991 Zoogeographic Provinces of the Humboldt, Benguela and Leeuwin Current systems. In: *The Leeuwin Current: an influence on the coastal climate and marine life of Western Australia*. (eds. AF Pearce and D I Walker). *J Roy Soc WA* 74:59-69.
- Pearce, A F 1986 Sea temperatures off Western Australia. *FINS* 19:6-8.
- Pearce, A F 1991 Eastern boundary currents of the southern hemisphere. In: *The Leeuwin Current: an influence on the coastal climate and marine life of Western Australia*. (eds. A F Pearce and D I Walker). *J Roy Soc WA* 74:35-45.
- Phillips R C & Menez E G 1988 Seagrasses. *Smithsonian Contributions to the Marine Sciences* 34: 1-103.
- Phillips R C, Santelices B, Bravo R & McRoy C P 1983 *Heterozostera tasmanica* (Martens ex Aschers) den Hartog in Chile. *Aquat Bot* 15: 195-200.
- Rochford D J 1975. Oceanography and its role in the management of aquatic ecosystems. *Proc Ecol Soc Aust* 8: 67-83.
- Rochford D J 1984 Effect of the Leeuwin Current upon sea surface temperatures off south-western Australia. *Aust J Mar Freshw Res* 35: 487-9.
- Santelices B, Castilla J C, Cancino J & Schmiede P 1980 Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in central Chile. *Mar Biol* 59: 119-132.
- Setchell W A 1935 Geographic elements of the marine flora of the North Pacific Ocean. *Amer Natur* 69: 560-577.
- Simpson C J & Masini R J 1986 Tide and seawater temperature data from the Ningaloo Reef Tract, Western Australia, and the implications for coral mass spawning. *Bulletin No. 253*, Department of Conservation & Environment, Perth. 18pp.
- Suto S 1950 Studies on the shedding, swimming and fixing of the spores of seaweeds. *Jap Soc Sci Fish Bull* 16: 1-9.
- Tomlinson P B 1974 Vegetative morphology and meristem dependence. The foundation of productivity in seagrasses. *Aquaculture* 4: 107-30.
- Walker D I, Kendrick G A & McComb A J 1988 The distribution of seagrasses in Shark Bay, Western Australia, with notes on their ecology. *Aquat Bot* 30: 305-317.
- Walker D I & Prince R I T 1987 Distribution and biogeography of seagrass species on the North-West Coast of Australia. *Aquat Bot* 29: 19-32.

Womersley H B S 1982 Aspects of the distribution and biology of Australian marine macroalgae. In: The Biology of Australian Plants (eds J S Pate & A J McComb) University of Western Australia Press. 294-306.

Womersley H B S 1984 The Marine Benthic Flora of Southern Australia. Pt. 1. (Government Printer: South Australia.)

Womersley H B S 1987 The Marine Benthic Flora of Southern Australia. Pt. II. (Government Printer: South Australia.)